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THE ORIGIN OF RAY TRACHEIDS IN THE CONIFERAEE

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(WITH SIXTEEN FIGURES)

Considerable attention has been devoted in recent years to the phylogenetic significance of ray tracheids in the Coniferae. PENHALLOW (1), arguing from their distribution and from his theory of their origin, concludes that the number in a given species is in direct proportion to its specialization, and that the forms where they are most numerous are derived from those where they are not so well developed. JEFFREY (2), on the other hand, from a study of certain traumatic phenomena, considers that the forms where they attain their greatest development, namely the pines, are the most ancestral, and have given rise by degeneration to the ones in which they occur sporadically. Apart from its intrinsic interest, it is hoped that the present study, by determining the origin of the ray tracheid, will supply a basis for its correct phylogenetic interpretation.

In carrying on the study, a thorough investigation was made of the character and mode of formation of the ray tracheid throughout the individual plant, but more especially in the primitive regions: seedling stem and root, young branch and young root of the adult, and the axis of the seed cone. The forms chosen for detailed investigation were our indigenous species of the hard and soft pines, *Pinus resinosa* and *P. Strobus*, but the results were confirmed in many other forms. The usual method was to follow a ray by means of a series of sections, from its beginning at the pith through the wood to the cambium.

The origin of the medullary ray at the pith has been described and figured by KNY (3) for *Pinus silvestris*. He states that in this region all the ray cells are parenchymatous, and elongated not radially but vertically. These long cells are often in connection with similar cells from rays lying above or below. Very soon they separate, shorten in the vertical direction, and elongate radially to form the typical medullary rays, which during their further course are separate. A later

writer, CONWENTZ (4), agrees with this description and extends it to include the root. I have found the observations of both writers to be practically true for *Pinus Strobus* and *P. resinosa*. In view of what is to follow, however, dissent must be expressed from the statement that during their further course the rays are separate. An important feature which neither writer emphasizes is that the rays in this young wood are low, rarely more than two cells in height.

The further course of the rays in root, stem, and cone axis shows essential differences; accordingly these regions are treated separately.

Root

Some distance from the pith certain peculiar tracheids appear, which KNY and other investigators seem to have overlooked.

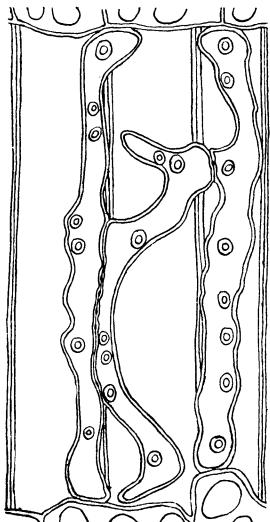


FIG. 1

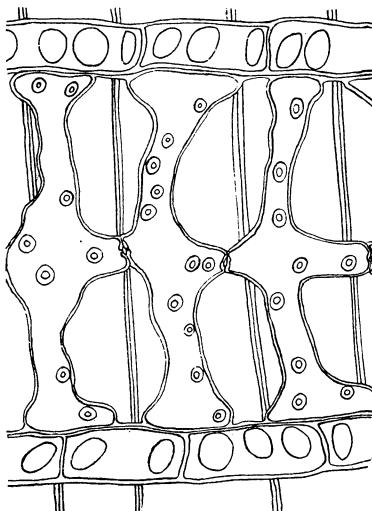


FIG. 2

FIGS. 1, 2.—Fig. 1, *P. resinosa*: young root; short tracheids extending between two rays; fig. 2, *P. Strobus*: young root; short tracheids with characteristic radial projections.

Examples of them are shown in figs. 1 and 2. They occur in radial rows, extending between two rays which lie in the same vertical plane. Consequently they are of various lengths, depending on the distance between the rays. Their form is also variable, often being quite uniform, like tracheids (fig. 1), often very irregular in outline.

A frequent peculiarity is the possession of arms (fig. 2) projecting radially either from the ends, or the middle, or from both, and meeting similar projections from their fellows. In this case the bodies of the cells are some distance apart. The walls of all these short tracheids are generally thinner, and their bordered pits much smaller than those of ordinary tracheids.

The usual sequence of these cells and their transformations toward the cambium are illustrated in fig. 3, which is a camera lucida drawing of two consecutive sections from a series of the root of *Pinus resinosa*. The cambium in this figure is toward the right (this orientation has been preserved throughout my illustrations). On their first appearance, toward the left of the figure, these tracheids have the more regular form approximating ordinary tracheids. Farther out they become irregular, usually with the above mentioned projections; then divisions occur, forming two superposed rows. These soon separate, taking up their position along the rays (center of figure) and forming irregular marginal cells, which gradually become regular and assume the form of true ray tracheids. In the ray at the bottom of the figure, ray tracheids have already been formed, but in one at the top this process has not yet been completed. In *Pinus Strobus* the sequence is similar. Often in both, the series is not so regular as the one just described; some stages may be hurried over, some greatly prolonged. In the one drawn, the transformation has taken place much more quickly than is usually the case, for the transitional stages may often be traced through several years' growth.

That these elements are indeed transitional is further shown in fig. 3 (*Pinus resinosa*) by the development on their walls of the dentations characteristic of the ray tracheids of the hard pines. When they first appear the elements are quite smooth, but as they assume more the shape and character of ray tracheids they acquire these dentations. One may often find intermediate cells whose walls are partly smooth like tracheids and partly dentate like ray tracheids (center of fig. 3).

It is evident that in the root of these forms we have a complete transition between short tracheids and ray tracheids; that by a process of division, of shortening, and of radial extension marginal ray tracheids have been produced from tracheary tissue.

The description so far has dealt with the marginal ray tracheids. The interspersed ones appear about the same time; their origin is illustrated in fig. 4. At the left of the figure are the irregular short tracheids extending between two rays. Farther to the left, that is, nearer the pith, these rays are more distant and the transitional tracheids are longer. To the right the rays gradually approach and

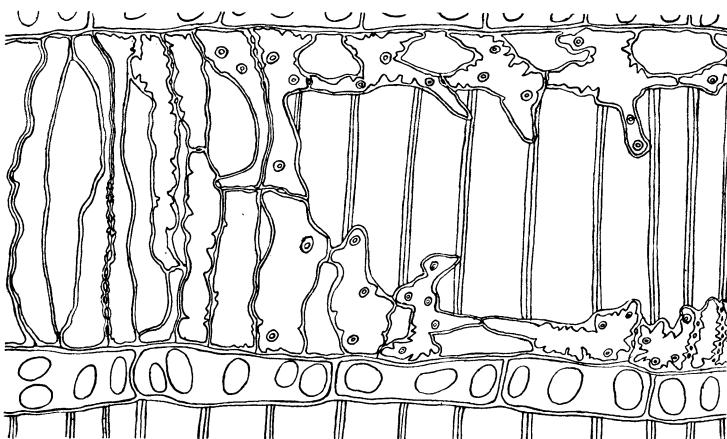
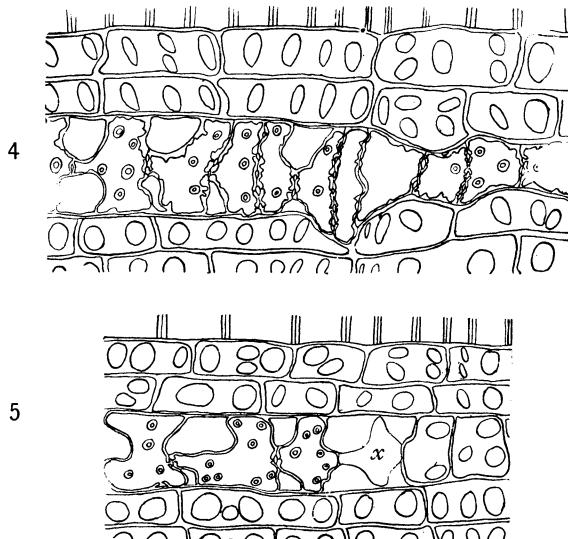


FIG. 3.—*P. resinosa*: young root; the transformation of short tracheids to marginal ray tracheids.

the tracheids shorten to form the regular interspersed ray tracheids which continue to the cambium. Thus interspersed ray tracheids originate from the same kind of tracheary element as the marginal ones. In the latter case the rays separate and the tracheids form along their margin. In the former, the rays draw together and the tracheids shorten and take their place in the center of the resulting composite ray.

The formation of this ray calls attention to an undescribed phenomenon apparently rather common in *Pinus*, namely the fusion of rays. As noted above, when the rays originate at the pith they are usually only one or two cells in height; but in the adult wood many of them are much higher. In the root wood up to twelve years old, careful observations were made to determine to what extent the increased height was due to fusion. This was done by following the rays in a series of sections from the cambium to the pith. It was found that

practically every one of the high rays was formed by a combination of two or more lower ones. Only very rarely was a height of four cells attained otherwise. The so-called *primary* rays are then really formed *secondarily*, by fusion. To what extent this fusion is characteristic of the other forms has not yet been determined, but it would seem that the low ray is the primitive condition in the pines.



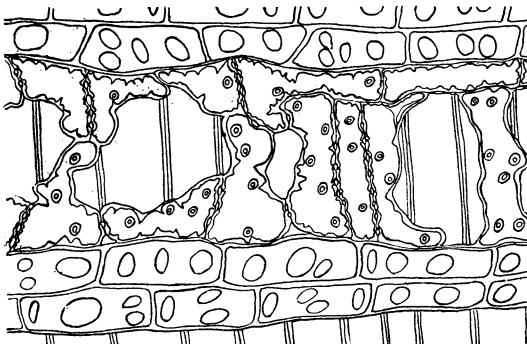
FIGS. 4, 5.—Fig. 4, *P. resinosa*: young root; the transformation of short tracheids to interspersed ray tracheids, and the fusion of rays; fig. 5, *P. Strobos*: young root; the replacement of ray tracheids by parenchyma; at *x* is a degenerating tracheid.

The approach of the rays does not always end in the production of one with interspersed tracheids. When the rays have drawn together till the intervening tracheids have formed true ray tracheids or are on the point of doing so, then these elements are often replaced by a row of parenchyma cells which soon assume the ordinary form and size. In fig. 5 at the left are the short transitional tracheids which are replaced at the right by high parenchyma cells. Farther toward the cambium these gradually become lower and indistinguishable from other cells of the ray.¹ Instances were also observed where the

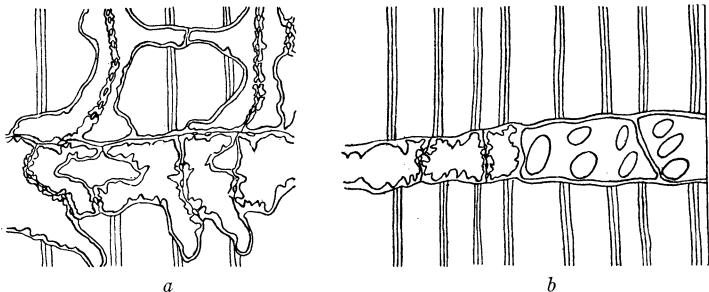
¹ In this drawing, and in the others as well, with the exception of figs. 8, 9, 14–16, the simple pitting of the wall of the parenchyma has been used to distinguish this tissue from the tracheary elements with their bordered pits, the nuclear and protoplasmic contents of the former being omitted.

fusion of rays eliminated a row of tracheids without replacement by parenchyma. The tracheids were simply "pinched" out, only the parenchyma cells continuing. In a few cases, even after true marginal ray tracheids had been formed as above indicated, the rays drew together and fused, with the result that the marginal ray tracheids were "pinched" out.

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7



FIGS. 6, 7.—Fig. 6, *P. resinosa*: young root; illustrating the formation of a double row of ray tracheids; fig. 7, *P. resinosa*: young root; formation of a wholly tracheidal ray, and its transformation into a parenchymatous one.

The origin of the marginal and interspersed ray tracheids and their relationship to the fusion of rays have been described. The more complicated case of the formation of two rows of tracheids on the margin of a ray is partly illustrated in fig. 6. At the left, toward the pith, are two rows of transitional tracheids touching end to end. Beyond the figure, nearer the medulla, these have been formed from a single row of longer tracheids. Toward the cambium the row on the

margin of the upper ray settles down to form regular ray tracheids while the other remains transitional. A repetition of the process in this row gives rise, beyond the figure, to a double series on the margin of the upper ray. In many cases, however, the second row is formed without the intervention of the transitional cells, this stage being either hurried over or completely omitted.

The only kind of ray tracheid whose formation has not yet been described is that composing the wholly tracheidal ray. When the rays are far apart, two or more divisions may take place in the long tracheids instead of the usual single one. Then one or more rows of transitional cells are formed midway between the rays, with other rows above and below, that is, touching the rays. When the latter rows separate from the central ones, these continue as irregular tracheidal cells which gradually become regular, forming a completely tracheidal ray. Fig. 7 represents only the ends of the series, a considerable space at the center being left out; in *a* are two rows of irregular tracheids, the lower of which settles down to form the completely tracheidal ray seen in *b*.

At the right in figure 7*b* another phenomenon is illustrated. This is the replacement of a tracheidal ray by a parenchymatous one. It is not an abnormality in this section, for numerous examples were seen. In fact it seems to be the common method of origin for secondary rays, that is for ones which do not run to the pith. Owing to the yearly increase in the circumference of the wood, many new parenchyma rays must be formed if the number in a given area is to remain at all constant, and it seems easier for them to be produced from cambial cells which give rise to ray tracheids than from longer ones which give rise to wood tracheids.

In the development of some of the ray tracheids at the cambium further evidence is afforded of the origin of these structures from tracheary tissue. In fig. 8 the cambium is at the right. It has just given off a tracheid whose upper end is

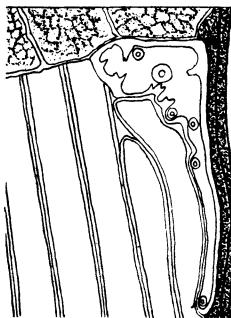
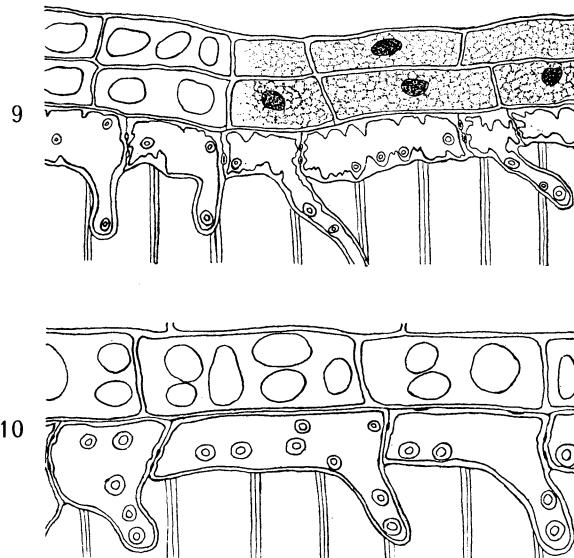


FIG. 8.—*P. resinosa*; young root; the development of a ray tracheid at the cambium.

"turning" along the ray and developing the buttresses characteristic of the ray tracheids of the hard pines. The lower part remains smooth. At this stage then, it is quite intermediate between a wood tracheid and a ray tracheid.

Farther from the cambium whole rows of tracheidal cells may be observed, each with a long tail-like projection extending from one



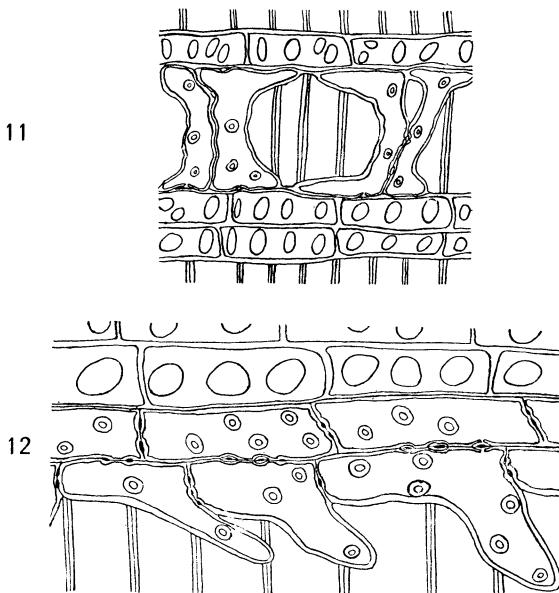
Figs. 9, 10.—Fig. 9, *P. resinosa*: young root; a row of ray tracheids with tail-like projections; fig. 10, *P. strobus*: adult root; ray tracheids with "tails."

end (fig. 9), and this end is always the one nearer the cambium. The "tail" is evidently the smooth part of the tracheid as seen at the cambium. Moreover, in *Pinus resinosa* the "tail" lacks the characteristic dentations present on the rest of the cell. Apparently then it is the result of an incomplete shortening of the tracheid. Fig. 10, from an old root of *Pinus strobus*, shows that these projections persist in the mature wood, but, as is to be expected, they are neither so numerous nor so conspicuous.

Stem

The root is admittedly more conservative than the stem. Accordingly in the latter the evolutionary processes are not so well repre-

sented. There is a hurrying over the early stages, so that an actual series can rarely be observed. Nevertheless, the transitional form of tracheid is occasionally found, and has been drawn in fig. 11 from the second year's growth of *Pinus Strobus*. Tail-like projections are quite common, and have been illustrated in fig. 12.



FIGS. 11, 12.—Fig. 11, *P. Strobus*: young stem; transitional tracheids; fig. 12 *P. Strobus*: adult stem; ray tracheids with "tails."

The only good stem series showing the transformation from tracheids to ray tracheids was observed in old stem wood of *Pinus resinosa* which had been wounded (fig. 13). The rapidly shortening series of tracheids ends at the right in true ray tracheids with buttressed walls. In this wounded material also the tail-like projections were very numerous and very large. Both features are to be accounted for as traumatic reversions similar to those described by JEFFREY for *Cunninghamia* (2), in which form though ray tracheids are not normally present they were found in connection with a wound.

Even in the normal adult ray tracheid, however, we find indications of its tracheary origin. One of these is the occurrence of tertiary

spirals. This has been described by BAILEY (5) for some species of *Pinus* as well as for *Picea* and *Pseudotsuga*. He states: "Ray tracheids appear to follow closely the wood tracheids. Where spirals

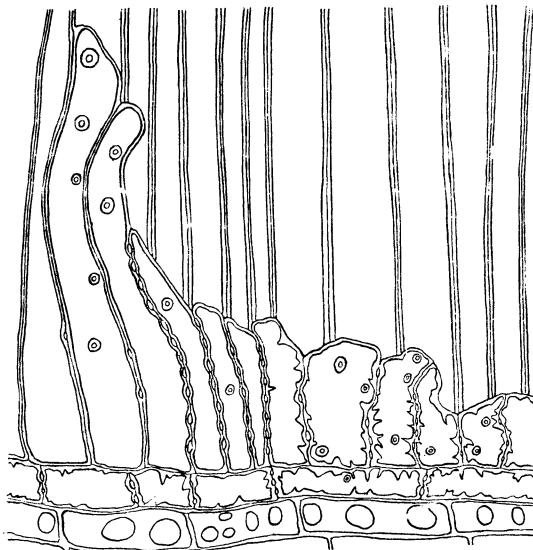


FIG. 13.—*P. resinosa*: adult stem; a series of tracheids from a wounded region, showing transformation to ray tracheids.

are strongly developed (summer wood) in the latter elements, they will also appear in the former." This concomitant occurrence of tertiary spirals on the elements in question argues community of origin.

Seedling

So far the study of the seedling has presented no features not observed in the corresponding regions of the adult, except that here the ray tracheids are later in appearing.

Cone axis

True ray tracheids are quite absent from the cone axis, as JEFFREY and CHRYSLER (6) have pointed out. I have found their place taken, however, by the bent ends of the tracheids. Fig. 14 shows a tracheid

whose end is bent along a ray for a remarkable distance. Such tracheids are very common in the cone axis, more than half the rays showing at least one in some part of their short course. Evidently they do the work of the ray tracheid, and probably represent the first step in a process of turning and shortening which, as described above, ends in the production of ray tracheids. Similar bent ends are sometimes to be found in the young stem, and are evidently to be interpreted in the same way.

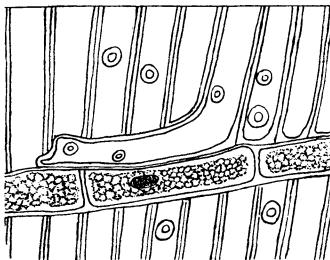


FIG. 14.—*P. Strobus*: cone axis: the end of a tracheid bent along a ray.

Relation to albuminous cells

In the light of what has been said of the origin of ray tracheids, an interesting circumstance is furnished by their relationship to the albuminous cells of the ray. STRASBURGER (7) points out the homology between the latter and sieve tubes. "The albuminous cells are higher than the ordinary cells of the ray and like sieve tubes have sieve areas, soon lose their contents, and ultimately collapse." They are then virtually *ray sieve tubes*. Now in the Abietineae, where ray tracheids are numerous, albuminous cells were always found conterminous with them through the cambial region. This is illustrated in fig. 15 even for a row of interspersed ones. In the Araucarineae and Taxaceae, where there are no ray tracheids, there are no albuminous cells. In those Taxodineae and Cupressineae where no ray tracheids were seen, no albuminous cells were found. And in *Thuja*, where ray tracheids occur sporadically, the only albuminous cells were those lining up with ray tracheids. Albuminous cells are then always associated with ray tracheids (an interesting exception is noted below). This association and their sieve tube character indicate that they bear the same relationship to ray tracheids as the sieve tubes to wood tracheids. They thus afford valuable collateral evidence of the tracheary origin of their representatives in the wood.

The exception referred to is found in *Abies balsamea*. Here almost every ray passing through the bast has albuminous cells on its margin,

but very few have ray tracheids. The albuminous cells are never in line with the parenchyma cells of the ray, but always above or below them. Often they are in line with two or three degenerating cells on the wood side. These facts support the view of JEFFREY (2) that the scarcity of ray tracheids in certain Abietineae, including *Abies*,

is the result of degeneration. The albuminous cells, elsewhere inseparable companions of the ray tracheids, persist, while the ray tracheids themselves have disappeared. The latter are probably represented by the degenerating cells mentioned.

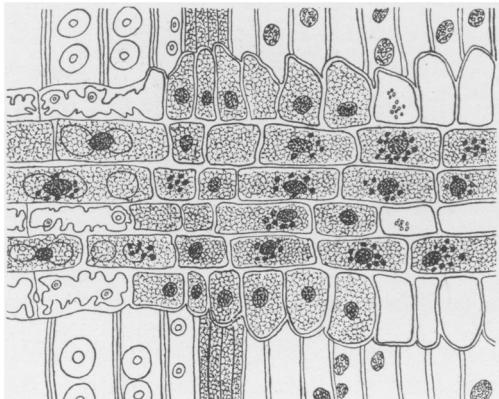


FIG. 15.—*P. resinosa*: old stem; cambial region showing albuminous cells in line with ray tracheids.

wounded root of *Abies amabilis*. Hitherto all observers have reported ray tracheids absent from the wood of this species. Yet in a piece of root wood which had been wounded several times, undoubtedly ray tracheids were developed in considerable numbers. This phenomenon parallels the traumatic revival of ray tracheids in *Cunninghamia* described by JEFFREY (2), and admits of a similar interpretation, in this case their ancestral presence in the genus *Abies*.

General considerations

The character and relationships of the ray tracheid have been described in the various regions of the individual plant. As has been shown, it is in the young root that the proof of its origin from tracheary tissue is most conclusive. Here transitions were observed from short tracheids extending between the rays to ray tracheids of all kinds. A significant feature, which has not yet been emphasized in connection with these transitional areas, is the occurrence of degenerating cells. One of these has been incidentally illustrated in fig. 5 at *x*. They

are structureless, shadowy outlines replacing transitional tracheids, which they resemble in form, although often somewhat more irregular. They occur in considerable numbers wherever the former elements are found, and are evidently to be regarded as "degeneration products," to which transitional structures are always subject. As such they emphasize the transitional character of the regions in question, and help to complete the chain of evidence for the origin of the ray tracheids from tracheary tissue.

PENHALLOW's argument (1) for his theory that ray tracheids are derived by modification from the parenchymatous cells of the ray, is the occurrence of ray tracheids conterminous with parenchyma cells. But this is so rare that DEBARY (8) was led to assert that it never occurred. I must confirm PENHALLOW's observation, however, especially in the young plant, where such an appearance is more common than in the adult. I have observed and figured this feature in the formation of secondary parenchymatous rays from wholly tracheidal ones (fig. 7), and in the replacement of interspersed ray tracheids by parenchyma (fig. 5). I have observed also a similar replacement of marginal ray tracheids by parenchyma cells. In these instances, however, it is to be noted that the parenchymatous cells are toward the cambium (to the right in the figures), and so *replace tracheary elements*, the reverse of what is required from PENHALLOW's point of view. This is indicated in the very figure which PENHALLOW uses to illustrate the fact that ray tracheids may abut on parenchyma cells (his figure is reproduced herewith, fig. 16). The direction in which the oblique end walls are inclined, and in which the tail-like projection points, which is seen on one of the ray tracheids on the top of the ray, indicates, as shown above (figs. 8-10, 12), that the cambium is to the left of his figure. The parenchyma cell which is in line

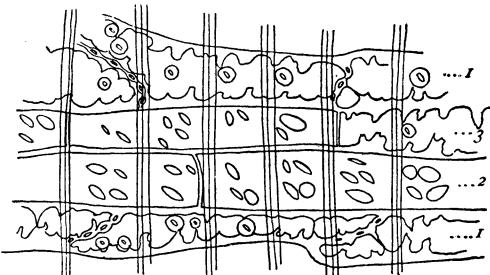


FIG. 16.—*P. serotina*: medullary ray showing (1) the ray tracheids with dentate walls, (2) the structure of the parenchyma cells, (3) tracheids conterminous with parenchyma cells.—From PENHALLOW (1).

with the ray tracheid is then nearer the cambium, and so what we really have is the replacement of a row of tracheary elements by parenchymatous ones. The origin of such a row of ray tracheids is to be looked for toward the pith, and, as I have shown above, the ray tracheids arise here either in connection with transitional tracheids, or, when these are omitted, above or below the ray and not in line with parenchyma cells.

The intimate study of the medullary ray from its beginning at the pith in the different regions of the individual plant, besides disclosing the origin of the various types of ray tracheid, has drawn attention to important features in the distribution of these structures. KNY has called attention to their absence in the first year's growth of the stem, and JEFFREY and CHRYSLER state that they are not present in the seed cone. In the young branch of *Pinus Strobus* they appear sporadically during the second and third years, and then increase slowly in number until the adult condition is attained after about ten years. In the seedling they are still later in appearing, as is also the case in the young root. In the latter region they never become so numerous as in the stem. In *Pinus resinosa* they appear in abundance much earlier and increase in number much more rapidly, reaching the adult condition in five or six years. They are never found in the cone axis of either species. Thus in the primitive regions of the plant ray tracheids do not occur, and therefore they must be regarded as specializations. That they are of cenogenetic origin is further indicated by the fact that in the older pines, the Pityoxyla of the Cretaceous, as described by JEFFREY and CHRYSLER (6), no ray tracheids occur.

In view of their origin and distribution, ray tracheids are regarded as specialized structures and their phylogenetic meaning so interpreted. Those woods in which they are most abundant are considered most modern, unless, as in *Abies*, it can be shown that they have been secondarily lost. Their character when present is as important as their number. For example, if the early growth shows many transitional elements or a large development of tail-like projections, then the wood is stamped as primitive. Again, the smooth-wall form in the soft pine is more tracheid-like and therefore more primitive than the dentate form of the hard pine, an inference which

is strengthened by the earlier and more rapid development of ray tracheids in *Pinus resinosa* than in *Pinus Strobus*.

Summary

1. In the young root complete transitions may be observed from short tracheids extending between the rays, to ray tracheids both marginal and interspersed. In the young stem only remnants of the transition usually remain. The complete series, however, may occur traumatically.

2. Further evidence of the origin of ray tracheids from tracheary tissue is found in (1) their development in the cambial region of the young plant, (2) the occurrence of tail-like projections, and (3) the possession of tertiary spirals.

3. The occurrence of ray tracheids bears a definite relation to that of albuminous cells.

4. In *Abies* the possession of albuminous cells and the traumatic occurrence of ray tracheids indicate that the latter are vestigial.

5. The regional and fossil distribution of ray tracheids indicates their ancestral absence in the pines.

6. The hard pines are more specialized than soft ones.

7. The large rays of *Pinus* are usually formed by the fusion of smaller ones.

8. Ray tracheids are often replaced by parenchyma cells. The importance of this in the formation of secondary parenchymatous rays has been indicated.

This study was undertaken at the suggestion of Mr. R. B. THOMPSON and carried on with his constant advice. My warmest thanks are due to him for quite exceptional kindness throughout the course of the work.

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